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Expectation of Genetic Alteration of Muscle Composition and Growth Traits in Rainbow Trout (Salmo gairdneri)

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EXPECTATION OF GENETIC ALTERATION OF MUSCLE COMPOSITION AND GROWTH TRAITS IN RAINBOW TROUT (SALMO GAIRDNERI)

BY

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EXPECTATION OF GENETIC ALTERATION OF MUSCLE COMPOSITION AND GROWTH TRAITS IN RAINBOW TROUT (SALMO GAIRDNERI)

This thesis is approved as a creditable and independent investigation by a candidate for the degree, Master of Science, and is acceptable for meeting the thesis requirements for this degree. Acceptance of this thesis does not imply that the conclusions are necessarily the conclusions of the major department.

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INTRODUCTION

The breeding of farm animals to produce superior organisms has been extensively applied in many parts of the world. Much of the research has been concerned with the manipulation of muscle protein and fat in muscle tissue for the purpose of catering to human needs (Kielanowski 1972; Dinkel and Busch 1973; Olson et al. 1976).

Though fishes are able to convert food to quality protein more efficiently than most animals, they have been underutilized as a protein source in the United States. Until recently, genetic manipulation through selection to enhance their quality has not been extensively applied (Smith and Rumsey 1976). Because of the increasing need for quality protein in the world, fish rearing, and subsequent character improvement should become a more important part of world protein production.

In order for fish production to be efficient, one basic requirement will be the production of an organism that will perform well in a hatchery condition (Gjedrem 1976). Artificial selection for increased growth, survivability, and disease resistance has been investigated in hatchery and wild strains of salmonids (Donaldson and Menasveta 1961; Aulstad et al. 1972; Gjedrem and Aulstad 1974; Kanis et al. 1976; Kincaid et al. 1976; Refstie et al. 1977). The use of wild strains, however, has been minimal due to their limited accessibility and poor performance in artificial rearing conditions (Reisenbichler and McIntyre 1977; Reinitz et al. 1979). The potential to increase or at least maintain genetic variability in hatchery

strains may increase their utilization.

Regulating the body composition of fish for a specific purpose will become an increasingly important requirement in fish production (Gjedrem 1976). Little is known about the degree of genetic influence (heritability) on body composition of fishes (Simon 1970), though it has been investigated in lab and farm animals (Dinkel and Busch 1973; Notter et al. 1976; Brown et al. 1977). Reinitz et al. (1979) found body composition differences among various strains of rainbow trout (Salmo gairdneri) and Gjedrem (1976) found differences in fillet quality among rainbow trout. Results from both these studies suggest potential for genetic improvement in this fish.

Genetic variation is believed to be 50% greater in fishes than in mammals (Ayala 1978). Gjedrem (1976) found coefficients of variation for economically important quality traits such as meat color and carcass score to average 30% in rainbow trout compared to 5-20% for similar characters in farm animals. Therefore increased genetic variability in addition to greater fecundity allow a greater potential for selective breeding among fishes than domestic livestock.

Phenotypic and genotypic correlations are important considerations when trying to alter the frequency of a particular trait in a population, for a change in one trait may have a pronounced effect on another (Falconer 1972). In selecting for body composition traits and overall quality improvement, it may also be more convenient and efficient not to select directly on the basis of composition analyses and taste testing but indirectly on the use of some more readily

available statistic such as weight. Reinitz et al. (1979) found a significant ($P < .01$) association between growth and percent protein on a dry weight basis. This suggests the possibility that direct selection for weight could bring about a measurable change in protein on a dry weight basis.

My objectives were to estimate heritabilities and phenotypic variances in rainbow trout for the traits: percent moisture, percent protein on a dry and wet weight basis, percent fat on a dry and wet weight basis, percent ash, standard length, weight, and K (condition factor). Another objective was to estimate phenotypic and genotypic correlations involving these traits. A final objective was to evaluate the potential for genetic alteration through direct and indirect selection of the above traits.

MATERIALS AND METHODS

Experimental Source

Rainbow trout reared under standard environmental conditions (Spring Standard Strain) at the U.S. Fish Genetic Laboratory, Beulah, Wyoming, were used in this study. Standard environmental conditions included water temperature, 11 ± 1 C, pH, 7.6 to 7.8, water hardness, approximately 420 ppm as $CaCO_3$ and 634 ppm total hardness. For further information on rearing see Kincaid et al. (1976).

At approximately 1 year of age 609 fish were killed and stored at -40 C for a period of 6 months, then filleted and refrozen for later analysis.

Preparation of Samples

Frozen fish fillets were homogenized in a Waring blender using dry ice. Aliquots were taken for the various analytical tests outlined below.

Protein

Total soluble protein was extracted from the fish sample using a modified version of the Ellis and Winchester method (1959). It involved the use of a 4% NaCl solution buffered with a 61:39 mixture of KH_2PO_4-K_2HPO_4 respectively (pH 7.0) which was diluted 1 to 20 parts with deionized water. The extraction solution was then blended with the sample for 6 intervals of 10 seconds each, pausing between intervals to prevent excessive protein denaturation. The processing took place in a temperature controlled room so that the blended solution temperature remained stable at 8 ± 2 C. This extract was

then centrifuged for 20 minutes at 0 C at 1000 x g. The supernatant represented the total soluble protein; the concentration of protein was determined by the biuret method (Snow 1950) and calibrated against the macro-Kjeldahl method (Horwitz 1975). Samples were run in duplicate and standardized with the use of a known aliquot of albumin.

Moisture and Ash

Moisture and ash determinations were estimated by the standard AOAC method (Horwitz 1975), where duplicate samples from the same muscle mass used for extraction, were dried at 135 C for 2 hours. Samples were then cooled in a vacuum desiccator and weighed. These dried samples were ashed in a muffle furnace at 600 C for 2 hours, cooled under vacuum as above, and weighed to obtain ash weight.

Fat

Fat estimations were calculated by subtraction of the percent moisture, protein, and ash from 100%. This was permitted by the minimal carbohydrate content of the muscle amounting to about 292 mg/g tissue (Black et al. 1966).

Experimental Design

A balanced heirarchal experiment was empolyed where each of 29 sires was mated to 3 dams for a total of 87 half-sib families. Seven progeny per dam were used for the analyses resulting in 609 observations. Appendix A lists the 29 sire sets and their distribution in the various tanks used.

Statistical Design

The statistical design for the estimation of heritability and

phenotypic and genotypic correlations was based on a hierarchal design conforming to the additive linear model:

$$Yijk = \mu + Si + Dij + Eijk \quad \text{(Becker 1975)}$$

where: Yijk = response of the kth observation in the jth dam in the ith sire.

μ = population of true mean.

Si = random effect of the ith sire.

Dij = random effect of the jth dam in the ith sire.

Eijk = random deviation of the response of the kth observation in the jth dam in the ith sire.

Assumptions underlying the analysis of variance and covariance needed in the unbiased estimation of heritability and correlations respectively, are first, that treatment and environmental effects are additive and second, that experimental errors are random and independent being normally distributed about a mean 0 with a common variance. The assumption of normality is required only in testing hypotheses (Steel and Torrie 1960).

To meet the above requirements, sires, dams, and progeny were chosen indiscriminately from a randomly mated reference population. At the time of analysis, full sib families were randomly selected and analyzed as families. "Batch" effects were minimized in protein determinations through use of an albumin standard in each family run. Common environmental effects during moisture and ash estimations were

considered minimal.

Test of normality (Snedecor and Cochran 1967) from skewness and kurtosis calculations were performed for all variables. This involved measuring deviation of the 29 sire set means from expectations of a normally distributed population. No significant departures from normality (2% level) were encountered.

Variances between progenies within sires within dams were tested for homogenity using a Chi Square test (Steel and Torrie 1960). Though percent protein on a dry weight basis and percent fat on a wet weight basis were the only variables whose null hypotheses of homogenity were not rejected, the average variance from 87 families with 6 degrees of freedom, represented a better estimate of the progeny variance than any single family estimate. Two transformations were used when they resulted in larger heritability value, represented a more normally distributed populalation, or resulted in a higher degree of homogenity among family estimated progeny variances.

Coded Variables

Traits examined were coded to facilitate their presentation (Table 1).

Heritability Estimations

Heritability values were estimated through the analysis of variance estimation of the sire variance component (σs^2), the dam variance component (σd^2), and the progeny variance component, (σp^2). Expected mean squares in a typical analysis of variance table are illustrated in Table 2.

Table 1. Code used in representing characters examined in rainbow trout.

CODE	DESCRIPTION
MOISTURE	percent moisture
DPROTEIN	percent protein on a dry weight basis
WPROTEIN	percent protein on a wet weight basis
ASH	percent ash
ASHLOG	$\log_{10}$ (ASH + 1)
DFAT	percent fat on a dry weight basis
WFAT	percent fat on a wet weight basis
LENGTH	standard length (snout to fork in tail) in millimeters
WTGMS	weight in grams of fish
K	condition factor of the fish calculated by: $\frac{\text{WTGMS X } 10^5}{(\text{LENGTH})^3}$
KLOG	$\log_{10}$(K)

Table 2. Typical analysis of variance of observed characters with expected mean squares.

SOURCE	EXPECTED MEAN SQUARES
Within sires	$\sigma_p^2 + 7\ \sigma_d^2 + 21\ \sigma_s^2$
Within dams within sires	$\sigma_p^2 + 7\ \sigma_d^2$
Within progeny	σ_p^2

Since the sire variance component in this case is equal to one-quarter of the additive genetic variance (covariance of half-sibs), the heritability by sire is equal to:

$$h_s^2 = \frac{4\ \sigma_s^2}{\sigma_s^2 + \sigma_d^2 + \sigma_p^2}$$ (Falconer 1972)

When referring to heritability I will be concerned with this estimate unless I state otherwise because it alone is unbiased (free of material and common environmental components).

Included in the dam variance component is not only one-quarter the additive genetic variance, but one-quarter the dominance variance and all the variance associated with common environmental effects (Falconer 1972).

$$h_d^2 = \frac{4\ \sigma_d^2}{\sigma_s^2 + \sigma_d^2 + \sigma_p^2}$$ (Falconer 1972)

An analysis of variance for each variable is presented in Appendix B.

Correlation Estimates

An analysis of covariance was used to determine phenotypic and genotypic correlations (Becker 1975). Estimations were obtained from the following formulas.

$$r_g = \frac{cov_{sxy}}{\sigma_{s_x}^2 \times \sigma_{s_y}^2}$$ (Becker 1975)

where:

r_g = genetic correlation

cov_{sxy} = covariance of sire involving variables x and y.

$\sigma_{s^2x \text{ or } y}$ = the variance of variable x or y associated with each sire.

$$r_p = \frac{cov_{Txy}}{\sigma_{T_x}^2 + \sigma_{T_y}^2}$$ (Becker 1975)

where:

r_p = phenotypic correlation.

cov_{Txy} = covariance of sires + dams + progeny involving variables x and y.

$\sigma_{T_x}^2$ or y = the variance of variable x or y associated with the total of sire, dam and progeny variance components.

An analysis of covariance for each variable combination follows the analysis of variance in Appendix B.

Genetic Advance Estimations

Genetic advance per year for trait x is defined below.

$$R_x = \frac{i h_x^2 \sigma_{p_x}}{L}$$ (Lush 1948)

where:

R_x = genetic response of x.

i = the intensity of selection

h_x^2 = heritability of x.

σ_{p_x} = phenotypic standard deviation of x.

L = generation interval or time between successive matings.

Correlated Response to Selection

The correlated response to trait y when selection is directed toward trait x is presented below.

$$CRy = ih_x h_y r_g \sigma_{p_y} \qquad \text{(Falconer 1972)}$$

where:

CRy	= correlated response of y.
i	= intensity of selection.
h_y	= square root of the heritability of y.
h_x	= square root of the heritability of x.
r_g	= genetic correlation between x and y.
σ_{p_y}	= phenotypic standard deviation of y.

RESULTS

Descriptive statistics including mean, range, variance, standard deviation, and coefficient of variation are given in Table 3. Transformed variables and their non-transformed counterparts are also shown. Variability measured as the coefficient of variation ranged from 2.14 for MOISTURE to 30.88 for WFAT.

The influence of the sire was examined for all variables in Table 4. MOISTURE, WPROTEIN, LENGTH, and KLOG had significant sire effects ($P < .005$).

Table 5 presents both sire and dam estimates of heritability along the diagonal for top left to bottom right. Genotypic and phenotypic correlations, within a calculated 90% confidence interval, are located above and below the diagonal respectively. DPROTEIN, ASHLOG, WFAT, and DFAT had heritability values of 0 while other traits had estimates ranging from a low of $0.48 \pm .223$ for MOISTURE to a high of $0.96 \pm .333$ for WTGMS. Genotypic correlations for DPROTEIN, ASHLOG, WFAT, and DFAT were not able to be estimated due to negative sire variance components associated with each of these variables. Because of large sample size, correlations as low as 0.08 were statistically significant ($P < .05$) though their importance at this level would be subject to the character under examination.

Table 3. Descriptive statistics of flesh composition, length, weight and condition traits.

VARIABLE	MEAN	VARIANCE	S.D.*	C.V.*	RANGE
MOISTURE	75.46	2.61	1.62	2.14	9.59
WPROTEIN	19.03	2.10	1.45	7.62	8.80
DPROTEIN	77.62	20.66	4.55	5.86	25.38
ASH	1.41	0.06	0.25	17.81	3.02
ASHLOG	0.38	0.002	0.04	11.10	0.49
WFAT	4.11	1.56	1.25	30.38	8.19
DFAT	16.67	21.53	4.64	27.84	26.48
LENGTH	198.26	406.61	20.17	10.17	148.00
WTGMS	141.87	1768.00	42.06	29.65	303.30
K	1.77	0.03	0.18	9.93	2.13
KLOG	0.25	.002	0.04	16.61	0.42

* standard deviation

** coefficient of variation which is equal to: $\frac{100\ (S.D.)}{MEAN}$

Table 4. F test examining the influence of sire on traits examined (Null hypothesis of no sire effect, df = 28, 58).

VARIABLE	F	P <
MOISTURE	2.365	.005
DPROTEIN	0.710	.100
WPROTEIN	2.637	.005
ASHLOG	0.868	.100
DFAT	0.654	.100
WFAT	0.586	.100
LENGTH	3.838	.005
WTGMS	4.128	.005
KLOG	2.802	.005

Table 5. Heritability and genotypic and phenotypic correlation estimations for the observed traits.

	1 MOISTURE	2 WPROTEIN	3 DPROTEIN	4 ASHLOG	5 WFAT	6 DFAT	7 LENGTH	8 WTGMS	9 HTCG
1	.48±.223 .64±.194	-.72 -.66** -.60	.15 .25** .35	-.45 -.36** -.27	-.52 -.44** -.35	-.42 -.25** -.15	-.42 -.33** -.24	-.50 -.41** -.32	-.36 -.26** -.16
2	-1.18**	.73±.316 1.02±.246	.46 .54** .61	.13 .23** .33	-.43 -.35** -.25	-.60 -.53** -.45	-.25 -.35** -.43	.34 .43** .51	.16 .26** .36
3	0	0	-.19±.171 1.62±.363	-.21 -.10** 0	-.95 -.94** -.93	-.97 -.96** -.95	-.02 .08* .19	0 .10* .20	-.06 .05 .15
4	0	0	0	-.05±.125 .82±.236	0	-.02 .08* .19	-.01 .10* .20	.01 .11** .22	-.04 .06 .17
5	0	0	0	0	-.24±.138 1.34±.321	.94 .95** .96	-.09 .01 .12	-.09 .01 .12	-.08 .03 .13
6	0	0	0	0	0	-.21±.159 1.54±.351	-.18 -.07 .03	-.19 -.09* .01	-.13 -.03 .08
7	-.66 -.59** -.52	.53 .60 .67	0	0	0	0	.93±.331 .64±.191	.92 .94** .95	-.22 -.11** .10
8	-.73 -.67** -.61	.69 .74 .79	0	0	0	0	.96 .97** .98	.99±.338 .59±.169	.10 .21** .30
9	-.65 -.58** -.61	.79 .83** .86	0	0	0	0	.24 .34** .43	.46 .54** .62	.54±.221 .47±.165

Heritability estimates are along the diagonal from top left to bottom right, sire estimate on top and dam estimate on bottom.

Phenotypic and genotypic correlations are above and below the diagonal respectively with 90% confidence intervals.

* represents statistically significant at the 5% level.

** represents statistically significant at the 1% level.

0 in genotypic correlations infers that the value could not be estimated.

DISCUSSION

Means

Body composition measurement means estimated are supported by Denton and Yousef (1976) in similarly aged rainbow trout with the exception of WFAT which was higher in their study at 7% versus 4% in this study. Groves (1970) states that fat content may be dependent upon feed type.

Variability

The low MOISTURE coefficient of variation (2.1) and high DFAT coefficient of variation (27.8) was similar to that reported in mice by Eisen et al. (1977). Work by Denton and Yousef (1976) produced similar coefficients of variation for MOISTURE, WPROTEIN, DPROTEIN, and ASHLOG in 12-month old rainbow trout.

The coefficient of variation of WTGMS was estimated to be 29.6 which agrees with Aulstad et al. (1972) using rainbow trout. It was considerably lower than the 70 and 40 estimates reported by Gjedrem (1975) for rainbow trout. Differences in values may depend upon how standardized the environmental conditions were when the estimates were made.

Heritability

For variables MOISTURE, WPROTEIN, ASHLOG, WFAT and DFAT, the estimations of heritability by dam were much higher than the sire estimates. Common environmental or maternal effects and dominance effects were probably responsible for this inflation, since the dam estimate contained not only the additive genetic variation, but also

the full amount of non-additive genetic variation (dominance) and 4 times the common environmental variation (Falconer 1972). "Batch" effects may partly be responsible for this inflation because samples were dried as family groups. Samples for protein determinations were extracted without reference to a family but "batch" or common environmental effects may have occurred because of further treatment of samples as a family unit in subsequent steps of the protein analysis. I would consider common environmental effects associated with rearing minimal since whole families were not contained in any one tank (Appendix A) although at early ages, families were in individual tanks.

Heritability estimation by sire of WTGMS and LENGTH were higher, 0.99 ± .338 and 0.93 ± .331 respectively, than that reported in the literature (Table 6). Dam estimates though for WTGMS and LENGTH, 0.58 ± .169 and 0.64 ± .181, respectively, appear to be more realistic approximations.

Chance and random drift were possible explanations for high sire, low dam estimations since the degrees of freedom associated with the sires were only 28 compared to 86 for dams. This explanation is supported by the small paternal effect expected in fish of 365 days of age.

I did visually examine the possibility for half-sib families to have density related differences since each tank had varying numbers of fish. Density differences have been observed to cause variations in growth (Brauhn et al. 1976). No such tendency was noted nor were

Table 6. Literature review of heritability estimates of traits examined.

ATTRIBUTE EXAMINED	GENERAL FINDING	h^2	AUTHOR, DATE
WTGMS	365 day old - good potential	0.58 ± 169*	Present study
		0.99 ± .338**	
	150 day old - good potential	0.26 - 0.29	Kincaid et al. 1976
		0.29	Aulstad et al. 1972
	Fingerlings - good potential	0.09 - 0.32	Aulstad et al. 1972
	Brood stock - good potential	0.21	Gall 1975
LENGTH	365 day old - good potential	0.64 ± .181*	Present study
		0.93 ± .331**	
	150 day old - good potential	0.37 ± .23	Aulstad et al. 1972
DPROTEIN			
WPROTEIN	None of the below have been examined until this		
WFAT	study. For results see Table 5.		
DFAT			
ASHLOG			

* Dam estimate

** Sire estimate

sire sets associated with specific tanks.

Unequal feeding of sire sets, creating a greater variance in growth between sire sets, was another possible explanation for high sire estimates of growth heritability. However, fish were fed by the method of Buterbaugh and Willoughby (1967) except that hatchery constants were inflated 20% in order to insure that fish were fed amply without discrimination (Kincaid et al. 1976).

WPROTEIN heritability was high (0.73 ± 0.316) compared to DPROTEIN (0). This difference might be the result of WPROTEIN being a function of the moisture content of fish. This is supported by the negative genetic correlation (r = -1.18) between MOISTURE and WPROTEIN.

The occurrence of cloudy samples (5%) in the biuret method of Snow (1950) may have been also responsible for the high heritability estimate of WPROTEIN. In determination, any artifact having a uniformily biased effect on a variable would introduce bias into the heritability estimate of that variable. This cloudiness seemed to be greatest in large fish. In examining the determination of WPROTEIN, the sample before centrification had a certain amount of denatured protein. This was a consequence of refreezing fish fillets, homogenization with dry ice, and subsequent blending in salt solution. Since it was determined in this study that large fish were expected to have less moisture and more protein on average, these samples might be associated with larger amounts of denatured protein. This could result in interferences with the separation of the supernant from the rest of the sample thus creating "cloudy" samples and inflation in

WPROTEIN heritability. This was supported by the observation that increased blending in salt solution and therefore increased denaturation, was associated with cloudy samples.

Moisture content alone might have been responsible for cloudy samples since MOISTURE was highly correlated with WTGMS ($r = -.41$). This would inflate WPROTEIN heritability and contribute to the dicotomy between WPROTEIN and DPROTEIN heritability estimations. This might be supported by the small positive correlation between DPROTEIN and WTGMS ($r = 0.1$, $P < .05$) which disagrees with the large negative correlation ($r = 0.95$, $P < .005$) between them found by Reinitz et al. (1979) in whole rainbow trout.

In an attempt to measure the significance of cloudy samples on the various estimations made, visibly cloudy samples were removed from the statistical procedure. Little difference was found in the estimations. Since some degree of cloudiness may have gone undetected, it cannot be ruled out in having some effect on the results.

Variables DPROTEIN, WFAT, DFAT, and ASHLOG had heritability estimations of 0. The results in Table 4 are in agreement where an F test involving the null hypothesis of no sire variance was not rejected. Most muscle composition traits would be expected to be under control of a large number of genes (Falconer 1972). Therefore the probability for low heritability values in these traits would be high. Of the 6 flesh composition characters examined only 2 had heritabilities over 0. My estimations of 0 may not only be due to a high probability of low values expected but also because of smaller

differences expected in body composition of fillets as compared to the whole fish. Imprecision in the determination of these traits could also be partly responsible for 0 estimations.

Since research in muscle composition estimates of heritability in trout is non-existent and because estimates in production animals have been primarily concerned with quality measurements versus quantitative measurement, comparison with past work is difficult. Dinkel et al. (1973) estimated heritability of marbling in beef cattle to be 0.24. Work with laboratory animals also offers some comparison. Notter et al. (1976) working with mice estimated heritability of lean gain to be 0.20 ± .12 and the efficiency of protein gain to be 0.20 ± .08.

Correlations

Growth in terms of WTGMS showed a significantly positive correlation ($P < .005$), genotypically and phenotypically with LENGTH and KLOG. This is not surprising since heavier fish are usually longer and plumper. Aulstad et al. (1972) reported a highly significant ($P < .05$) phenotypic correlation of 0.94 between WTGMS and LENGTH in 150-day-old rainbow trout.

WTGMS showed a significantly negative ($P < .005$) correlation, genotypically and phenotypically with MOISTURE and a significantly positive ($P < .005$) association with WPROTEIN. The negative association of growth and percent moisture was partially supported by Denton and Yousef (1976) who found that as rainbow trout increased in age and size, percent moisture decreased and percent protein on a wet weight basis increased in whole body analysis. Reinitz et al. (1979)

found no significant association between growth and percent moisture in 180-day-old whole rainbow trout.

My results indicated a statistically significant ($r = 0.10$, $P < .05$) phenotypic correlation between DPROTEIN and WTGMS. Reinitz et al. (1979) however, found a highly significant ($P < .005$) negative correlation between them. One explanation for the discrepancy may be due to their examination of whole fish. Another may be due to the possible inflation in WPROTEIN estimations caused by cloudy samples.

The phenotypic correlation will be used in discussing the variables DPROTEIN, ASHLOG, WFAT, and DFAT because the genotypic correlation could not be estimated due to negative sire variance components associated with these variables.

ASHLOG was significantly positively correlated with WTGMS ($r = 0.1$, $P < .01$). This was in partial agreement with Denton and Yousef (1976) who found an increase in ash content with age and therefore growth.

WFAT was not associated with WTGMS but DFAT was significantly correlated with WTGMS ($r = 0.09$, $P < .05$). Denton and Yousef (1976) found an increase in total fat content as fish grew in age. Kownacki et al. (1977) found a positive correlation between percent fat on a dry weight basis and growth in female mice ($P < .05$), but not in male mice. This suggests that flesh composition correlations may be best estimated in fish by separate consideration of each sex.

An inverse relationship was found between MOISTURE and both DFAT and WFAT. These results were supported by Gerking (1955), and Lagler

et al. (1962) in fish and Lang and Legates (1969), Sutherland et al. (1974) and Eisen et al. (1977) in mammals. Groves (1970) found no significant correlation in whole salmonids.

MOISTURE was positively associated with DPROTEIN and DFAT and WFAT were inversely proportional to protein content. These findings are in agreement with Reinitz et al. (1979) and Reinitz et al. (1978) respectively. Groves (1970) found no significant ($P < 0.05$) correlation between fat percentage and protein, ash or moisture percentages in sockeye salmon (Oncorhynchus nerka). Reinitz's et al. (1979) and Groves' (1970) lack of associations may be due to the analyses of whole fish in smaller numbers compared to the present analyses of large numbers of fillets.

Efficiency of Protein Utilization

I have estimated the parameters, heritability, the phenotypic standard deviation, and the genetic correlations necessary to evaluate the genetic response of WTGMS, WPROTEIN, DPROTEIN, ASHLOG, WFAT, DFAT, LENGTH, and KLOG to selection. Before estimating genetic advance in these traits, it is important not only to re-emphasize that fish efficiently convert feed to edible protein but to explain why they do.

High efficiency in feed utilization by fishes is due to low energy cost of support and movement in water, their poikilothermous physiology and their efficiency of protein metabolism and nitrogen excretion (Smith and Rumsey 1976). The efficiency of protein utilization by fishes surpasses all other vertebrates.

About 30% of the gross energy of protein is unavailable to mammalian homeotherms because energy is needed for protein breakdown, the formation of urea or uric acid in the liver, and the concentration and excretion of this waste by the kidneys (Smith and Rumsey 1976). This amounts to a cost of 4 to 6 moles of ATP (88.4 to 122.6 kcal) per mole of urea or uric acid synthesized. Fish forego this production and concentration by excreting ammonia through the gills.

The energy cost of animal protein production in terms of feed per gain ratio is illustrated below (Table 7). Rainbow trout are the most efficient producers, having the smallest feed per gain ratio. Although fish gain is premised on the need for high levels of protein in their feed, their ability to utilize "low grade" or humanly unacceptable protein makes fishes an effective world protein source (Smith and Rumsey 1976).

Table 7. Energy cost of animal production.*

FOOD PRODUCT	FEED/GAIN RATIO	GRAMS PROTEIN/MCAL D.P.**
BEEF	8	2.3
PORK	4	6.4
BROILERS	2.1	15.9
RAINBOW TROUT	1.2 - 1.5	30 - 40

* Table taken from Smith and Rumsey (1976).

** Mcal digestible protein.

Expectation of Genetic Alteration through Selection

It appears that the characters LENGTH, WTGMS, and KLOG would respond to selection quickly due to their relatively high heritabilities and variances. This was supported by Kincaid et al. (1976) who found that after 3 generations of selection for growth in rainbow trout, genetic gain in weight amounted to 30.1%.

DPROTEIN, ASHLOG, WFAT, and DFAT are not heritable so genetic alteration through selection would be slight. The high phenotypic standard deviation associated with WFAT and DFAT must then be explained by environmental and non-additive genetic variance. This is supported by Eisen et al. (1977) who hypothesized fat deposition in mice to be partially controlled by directional dominance. Environmental manipulation through diet control has been found to be directly related to DFAT levels in fish (Groves 1970 and others).

MOISTURE and WPROTEIN are highly heritable with relatively low phenotypic standard deviations. One method of improving these traits would be mass selection or with family selection where a portion of fish muscle could be removed for analysis without death to the fish. A second method of improvement would be random sampling within families where selection of parents for the next generation would be based on family mean. These sampled fish could be killed. A third method would be indirect selection involving selecting directly for one trait with the expectation of changing another.

Indirect selection has its advantages when applying direct selection for the desired trait is difficult (Falconer 1972). Using

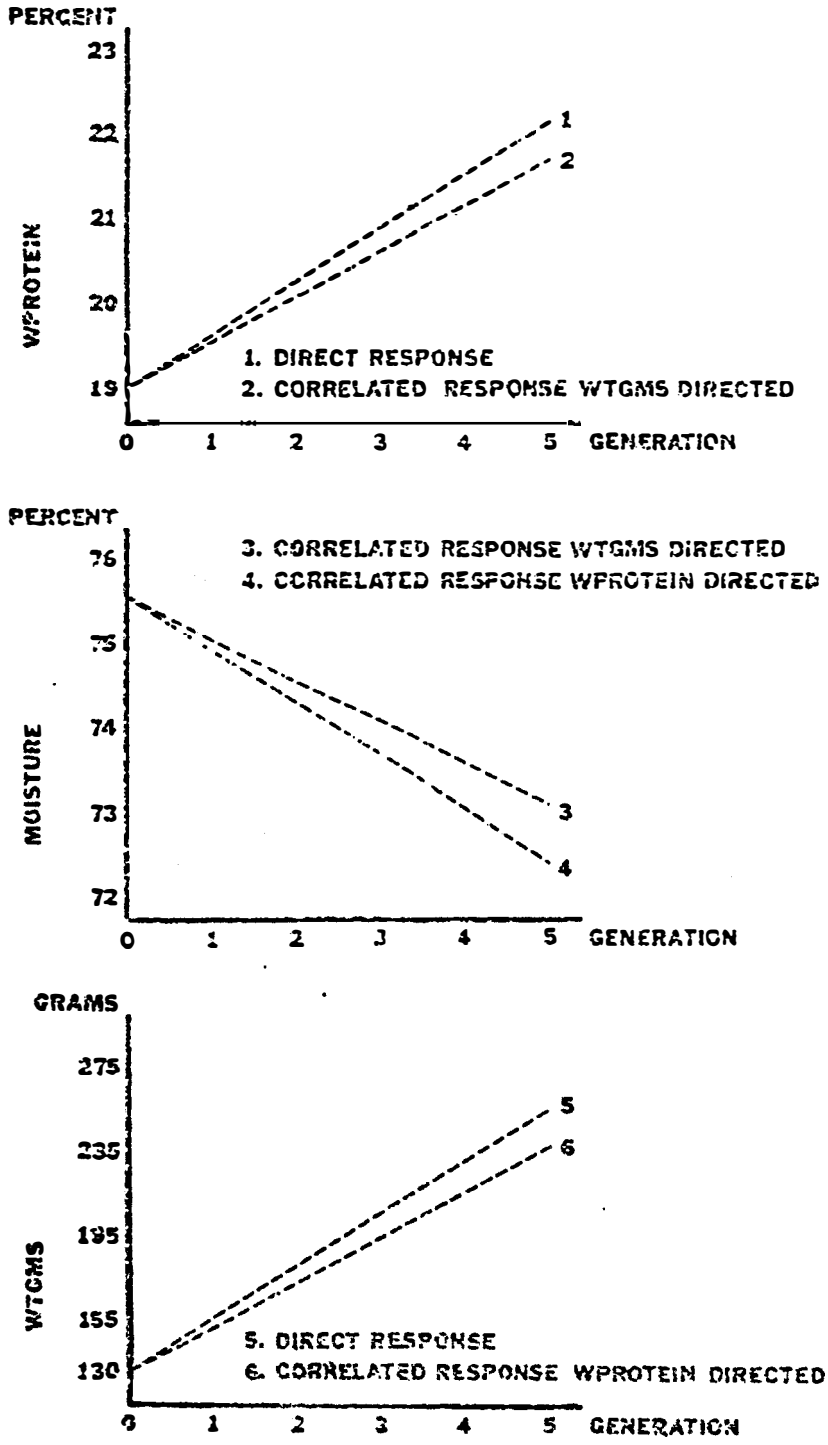
biopsy to determine composition levels may be more time consuming or possibly technically unfeasible in a hatchery. In order for indirect selection to be considered advantageous, a high genetic correlation is needed between the primary and secondary trait. Also, the secondary character must have a higher heritability than the primary trait (Falconer 1972). Indirect selection of WPROTEIN through direct selection of WTGMS using the sire estimate of heritability for WTGMS satisfies these requirements.

A selection model was solved using a 90% culling intensity (i = 1.78) (Falconer 1972) and sire estimates of heritability for 5 generations assuming a 3-year generation interval. Selection was directed separately toward both WTGMS and WPROTEIN for the purpose of examining the efficiency of genetic alteration in WPROTEIN, WTGMS and MOISTURE. When selection was based on WPROTEIN, the increases in WPROTEIN, WTGMS, and MOISTURE were 3.2%, 78.49g, and 2.9% respectively after 5 generations. When selection was based on WTGMS, the increases in WPROTEIN, WTGMS and MOISTURE were 2.7%, 123.53 gms, and 2.2% respectively after 5 generations (Figures 1, 2, and 3).

If selection for WPROTEIN could achieve as high a selection intensity as selection for WTGMS, the genetic gain in WPROTEIN would be only slightly greater than indirect selection through WTGMS. Also the total protein content of the fish would be greater in direct selection for WTGMS since WTGMS was approximately 40% larger than it would be through direct WPROTEIN selection. It may be argued that when selecting for increased growth and therefore increased WPROTEIN,

selection may be directed toward greater food consumption not higher feed efficiency. Simon (personal communication) has stated that in all strains of rainbow trout that he has examined for growth, all showed positive correlation between food conversion efficiency and body weight.

Figure 1. Response of WTGMS, WPROTEIN, and MOISTURE to selection directed toward either WTGMS or WPROTEIN.



CONCLUSION

One would expect selection for changes in WFAT, DFAT, DPROTEIN, and ASHLOG to proceed slowly because of low additive genetic variance associations. Any change in these components would have to be done through environmental manipulation such as diet regulation. Providing inbreeding is kept low through the use of large parental numbers, selection for WTGMS would be expected to proceed rapidly with a subsequent increase in WPROTEIN, LENGTH and KLOG and a decrease in MOISTURE. Having the power to alter these characters, man will be able to optimize their use for his specific needs.

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Appendix A. Distribution of half-sib families (sire sets) in tanks at 147 to 363 days of age.

TANK NUMBER	SIRE SET NUMBERS
5 and 29	1 3
6 and 30	1 2 3
7 and 31	2
8 and 32	1 2 3
9 and 33	4 5 6
10 and 34	4 5 6
11 and 35	4 5 6
13 and 37	7 8 9 10 11 12 13
14 and 38	7 8 9 10 11 12 13
15 and 39	7 8 9 10 11 12 13
16 and 40	11 12
17 and 41	14 16 18 19 20
18 and 42	14 15 16 17 18 19 20
19 and 43	15 16 17 20
21 and 45	21 22 23 24 25 26 27
22 and 46	21 22 23 24 25 26 27
23 and 47	21 22 23 24 25 26 27
49 and 50	28 28 28 29 29 29

29 sire sets were used out of a possible 56 sets. Though it appears that tank density was not uniform, unused sire sets made density distribution fairly equal.

Appendix B. Analysis of variance and covariance for the observed traits.

ANALYSIS OF VARIABLE MOISTURE

VARIANCE SOURCE	D.F.	SUM OF SQUARES	MEAN SQUARES	VARIANCE COMPONENT	PERCENT
TOTAL	608	1565.45650	2.60750	2.62195	100.00
SIRE	28	319.53260	11.41188	0.31360	11.96
DAM	58	279.92049	4.82622	0.41364	16.01
ERROR	522	985.90531	1.88871	1.88871	72.03

MEAN 75.460016
STANDARD DEVIATION 1.374303
COEFFICIENT OF VARIATION 0.018212

ANALYSIS OF VARIABLE NPROTEIN

VARIANCE SOURCE	D.F.	SUM OF SQUARES	MEAN SQUARES	VARIANCE COMPONENT	PERCENT
TOTAL	606	1278.49143	2.10278	2.12093	100.00
SIRE	28	363.56246	13.15580	0.36859	18.34
DAM	58	289.36511	4.98905	0.54284	25.59
ERROR	522	620.76386	1.18920	1.18920	56.07

MEAN 19.031284
STANDARD DEVIATION 1.090506
COEFFICIENT OF VARIATION 0.057295

ANALYSIS OF VARIABLE DPROTEIN

VARIANCE SOURCE	D.F.	SUM OF SQUARES	MEAN SQUARES	VARIANCE COMPONENT	PERCENT
TOTAL	606	12958.01137	20.66462	21.69829	100.00
SIRE	28	1429.66641	51.05116	-0.99075	0.0
DAM	58	4167.72775	71.85738	8.36035	38.54
ERROR	522	5960.83720	11.33494	13.33494	61.46

MEAN 77.623350
STANDARD DEVIATION 3.691303
COEFFICIENT OF VARIATION 0.047544

Appendix B. Continued

ANALYSIS OF VARIABLE ASH

VARIANCE SOURCE	D.F.	SUM OF SQUARES	MEAN SQUARES	VARIANCE COMPONENT	PERCENT
TOTAL	608	38.34670	0.06307	0.06394	100.00
SIRE	28	3.522e3	0.12581	-0.00076	0.0
DAM	58	8.22655	0.14184	0.01298	20.31
ERROR	522	26.59751	0.05095	0.05095	79.69

MEAN	1.409918
STANDARD DEVIATION	0.225729
COEFFICIENT OF VARIATION	0.160100

ANALYSIS OF VARIABLE MEAT

VARIANCE SOURCE	D.F.	SUM OF SQUARES	MEAN SQUARES	VARIANCE COMPONENT	PERCENT
TOTAL	608	950.20822	1.56297	1.65958	100.00
SIRE	28	76.67491	2.60932	-0.09456	0.0
DAM	58	276.14614	4.76062	0.52267	31.49
ERROR	522	593.46717	1.13691	1.13691	68.51

MEAN	4.115041
STANDARD DEVIATION	1.266240
COEFFICIENT OF VARIATION	0.259113

ANALYSIS OF VARIABLE FAT

VARIANCE SOURCE	D.F.	SUM OF SQUARES	MEAN SQUARES	VARIANCE COMPONENT	PERCENT
TOTAL	608	15094.16939	21.05650	22.77191	100.00
SIRE	28	1328.12048	47.43287	-1.19289	0.0
DAM	58	4204.05279	72.49367	8.23529	36.38
ERROR	522	7562.01620	14.48662	14.48662	63.62

MEAN	16.657459
STANDARD DEVIATION	3.809127
COEFFICIENT OF VARIATION	0.228681

Appendix B. Continued

ANALYSIS OF VARIABLE LENGTH

VARIANCE SOURCE	D.F.	SUM OF SQUARES	MEAN SQUARES	VARIANCE COMPONENT	PERCENT
TOTAL	608	0.2472200 06	0.4066120 03	0.4104020 03	100.00
SIRE	28	76023.77340	2715.13478	95.60689	23.30
DAM	58	41026.19048	707.34811	65.42576	15.94
ERROR	522	0.1301700 06	0.2493680 03	0.2493680 03	60.76

MEAN	198.262726
STANDARD DEVIATION	15.791384
COEFFICIENT OF VARIATION	0.079649

ANALYSIS OF VARIABLE WIGHS

VARIANCE SOURCE	D.F.	SUM OF SQUARES	MEAN SQUARES	VARIANCE COMPONENT	PERCENT
TOTAL	608	0.1075450 07	0.1768900 04	0.1785570 04	100.00
SIRE	28	0.3338470 06	0.1192310 05	0.4302100 03	24.09
DAM	58	0.1675440 06	0.2888690 04	0.2555550 03	14.31
ERROR	522	0.5746090 06	0.1099810 04	0.1099810 04	61.59

MEAN	141.367159
STANDARD DEVIATION	33.163338
COEFFICIENT OF VARIATION	0.234763

ANALYSIS OF VARIABLE K

VARIANCE SOURCE	D.F.	SUM OF SQUARES	MEAN SQUARES	VARIANCE COMPONENT	PERCENT
TOTAL	608	18.81497	0.03094	0.03109	100.00
SIRE	28	3.21050	0.11466	0.00324	10.42
DAM	58	2.70556	0.04664	0.00313	10.08
ERROR	522	12.89620	0.02471	0.02471	79.50

MEAN	1.771572
STANDARD DEVIATION	0.157192
COEFFICIENT OF VARIATION	0.088715

Appendix B. Continued.

ANALYSIS OF VARIABLE XLOG

VARIANCE SOURCE	D.F.	SUM OF SQUARES	MEAN SQUARES	VARIANCE COMPONENT	PERCENT
TOTAL	508	1.01915	0.00168	0.00169	100.00
SIRE	28	0.20625	0.00737	0.00023	13.37
DAM	58	0.15275	0.00263	0.00020	11.69
ERROR	522	0.66016	0.00126	0.00126	75.03

MEAN	0.246452
STANDARD DEVIATION	0.035562
COEFFICIENT OF VARIATION	0.144296

ANALYSIS OF VARIABLE ASHLOG

VARIANCE SOURCE	D.F.	SUM OF SQUARES	MEAN SQUARES	VARIANCE COMPONENT	PERCENT
TOTAL	608	1.08067	0.00176	0.00181	100.00
SIRE	28	0.10694	0.00382	-0.00003	0.0
DAM	58	0.25409	0.00440	0.00043	23.86
ERROR	522	0.71874	0.00138	0.00138	76.14

MEAN	0.379878
STANDARD DEVIATION	0.037106
COEFFICIENT OF VARIATION	0.097680

COVARIANCE OF VARIABLE MOISTURE WITH MPROTEIN

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	608	-942.637233	-1.550390	0.0	0.0	-0.6621
SIRE	28	-504.719119	-18.861397	-0.411229	-1.1775	-0.8864
DAM	58	-129.034066	-2.225588	-0.178523	-0.3740	-0.4536
ERROR	522	-509.434529	-0.975927	-0.975927	-0.6512	-0.6512

Appendix B. Continued.

COVARIANCE OF VARIABLE MOISTURE WITH PROTEIN

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	605	1141.534166	1.877523	2.525520	0.3362	0.2558
SIRE	20	-220.290962	-8.193249	-0.674467	0.0	-0.3378
DAM	58	348.612686	6.010564	0.579174	0.3092	0.3828
ERROR	522	1021.212443	1.956346	1.956346	0.3698	0.3898

COVARIANCE OF VARIABLE MOISTURE WITH ASH

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	603	-84.023879	-0.136197	0.005915	0.0144	-0.3408
SIRE	20	-6.540585	-0.233592	0.005915	0.0	-0.1950
DAM	58	-20.752957	-0.357810	-0.035590	-0.4822	-0.4325
ERROR	523	-56.730357	-0.108679	-0.108679	-0.3503	-0.3503

COVARIANCE OF VARIABLE MOISTURE WITH WEAT

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	608	-552.028750	-0.907942	0.078509	0.0576	-0.4497
SIRE	20	-13.169569	-0.470342	0.070509	0.0	-0.0631
DAM	58	-122.984310	-2.119040	-0.188684	-0.4033	-0.4405
ERROR	522	-415.954871	-0.796648	-0.796648	-0.5438	-0.5438

Appendix B. Continued.

COVARIANCE OF VARIABLE MOISTURE WITH OFAT

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	606	-1134.063872	-1.864223	0.535859	0.0758	-0.2496
SIRE	28	179.744353	6.419441	0.585859	0.0	0.2759
DAM	58	-341.244490	-5.883526	-0.574175	-0.3079	-0.3146
ERROR	522	-973.165714	-1.864302	-1.864302	-0.3564	-0.3564

COVARIANCE OF VARIABLE MOISTURE WITH LENGTH

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	606	-6579.772627	-10.859194	0.235320	0.0072	-0.3324
SIRE	28	-2084.522151	-74.447220	-3.246634	-0.5929	-0.4229
DAM	58	-363.539048	-6.267915	0.235320	0.0449	-0.1073
ERROR	522	-4131.711429	-7.915156	-7.915156	-0.3647	-0.3647

COVARIANCE OF VARIABLE MOISTURE WITH WTGMS

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	603	-16988.425672	-27.941490	0.0	0.0	-0.4114
SIRE	28	-5364.958814	-191.605672	-7.814085	-0.6727	-0.5194
DAM	58	-1595.571571	-27.509889	-1.185624	-0.1145	-0.2330
ERROR	522	-10027.893286	-19.210524	-19.210524	-0.4215	-0.4215

Appendix B. Continued.

COVARIANCE OF VARIABLE MOISTURE WITH K

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	608	-41.166319	-0.067708	0.0	0.0	-0.2384
SIRE	28	-14.762071	-0.527217	-0.017594	-0.5520	-0.4609
DAM	58	-9.149533	-0.157751	-0.011814	-0.4912	-0.3325
ERROR	522	-17.254714	-0.033055	-0.033055	-0.1530	-0.1530

COVARIANCE OF VARIABLE MOISTURE WITH KLOG

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	608	-10.478985	-0.017230	0.0	0.0	-0.2606
SIRE	28	-3.961323	-0.141476	-0.004911	-0.5842	-0.4800
DAM	58	-2.224371	-0.038351	-0.004305	-0.4752	-0.3492
ERROR	522	-4.290391	-0.008219	-0.008219	-0.1682	-0.1682

COVARIANCE OF VARIABLE MOISTURE WITH ASHLOG

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	608	-15.044159	-0.024744	0.001355	0.0197	-0.3635
SIRE	28	-1.065278	-0.038046	0.001355	0.0	-0.1622
DAM	58	-3.857249	-0.066504	-0.006731	-0.5003	-0.4556
ERROR	524	-10.121632	-0.019313	-0.019313	-0.3807	-0.3832

Appendix B. Continued.

COVARIANCE OF VARIABLE WPROTEIN WITH OPROTEIN

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	608	2208.875500	3.633019	3.633293	0.5393	0.5513
SIRE	28	532.689798	19.024634	0.270601	0.0	0.7341
DAM	58	764.692686	13.174012	1.632387	0.7663	0.6958
ERROR	522	912.093057	1.747305	1.747305	0.4388	0.4388

COVARIANCE OF VARIABLE WPROTEIN WITH ASH

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	608	50.125364	0.082443	0.082609	0.2243	0.2264
SIRE	28	5.139648	0.183523	0.001207	0.0	0.1427
DAM	58	9.174267	0.158177	0.012796	0.1524	0.1880
ERROR	522	35.812400	0.068606	0.068606	0.2787	0.2787

COVARIANCE OF VARIABLE WPROTEIN WITH WFAT

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	608	-380.116782	-0.625192	0.027654	0.0143	-0.3449
SIRE	28	-63.758015	-2.278143	0.027654	0.0	-0.3747
DAM	58	-166.058710	-2.863081	-0.367587	-0.6907	-0.5853
ERROR	522	-150.279057	-0.287874	-0.287874	-0.2475	-0.2476

Appendix B. Continued.

COVARIANCE OF VARIABLE WPROTEIN WITH DFAT

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	608	-2176.204519	-3.579284	0.0	0.0	-0.5319
SIRE	28	-472.241285	-16.865760	-0.185832	0.0	-0.6752
DAM	58	-751.871262	-12.963298	-1.591338	-0.7504	-0.6617
ERROR	522	-952.091971	-1.823931	-1.823931	-0.4394	-0.4394

COVARIANCE OF VARIABLE WPRGTEIN WITH LENGTH

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	608	6105.194540	10.041438	10.176290	0.3449	0.3484
SIRE	28	2580.644548	92.165877	3.674123	0.6025	0.4877
DAM	58	870.538571	15.009266	1.417853	0.2379	0.2527
ERROR	522	2654.011429	5.084313	5.084313	0.2952	0.2952

COVARIANCE OF VARIABLE WPROTEIN WITH WEGMS

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	608	15927.093681	26.195878	26.547067	0.4314	0.4295
SIRE	28	6735.613443	240.557623	9.613876	0.7433	0.6074
DAM	58	2242.640667	38.666218	3.622038	0.3075	0.3221
ERROR	522	6948.839531	13.311953	13.311953	0.3681	0.3681

Appendix B. Continued.

COVARIANCE OF VARIABLE WPROTEIN WITH K

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	608	36.765756	0.060470	0.061463	0.2394	0.2371
SIRE	28	18.616794	0.664957	0.028816	0.8119	0.5414
DAM	58	3.469478	0.059819	0.004529	0.1098	0.1240
ERROR	522	14.677486	0.028118	0.028118	0.1640	0.1640

COVARIANCE OF VARIABLE WPROTEIN WITH KLOG

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	608	9.410106	0.015477	0.015742	0.2633	0.2607
SIRE	28	4.951464	0.176838	0.007728	0.8255	0.5681
DAM	58	0.844190	0.014555	0.001090	0.1058	0.1270
ERROR	522	3.614451	0.006924	0.006924	0.1785	0.1785

COVARIANCE OF VARIABLE WPROTEIN WITH ASHLOG

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	608	8.585698	0.014121	0.014364	0.2320	0.2319
SIRE	28	0.678165	0.024147	-0.000827	0.0	0.1077
DAM	58	1.676711	0.028909	0.002424	0.1584	0.1952
ERROR	522	6.232680	0.011940	0.011940	0.2951	0.2951

Appendix B. Continued.

COVARIANCE OF VARIABLE OPROTEIN WITH ASH

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	608	-57.703233	-0.094907	0.021813	0.0165	-0.0832
SIRE	28	-0.128166	-0.004577	0.021813	0.0	-0.0018
DAM	58	-24.834081	-0.462657	-0.057681	-0.1751	-0.1449
ERROR	522	-30.740986	-0.058891	-0.058891	-0.0714	-0.0714

COVARIANCE OF VARIABLE OPROTEIN WITH WEAT

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	608	-3250.739784	-5.346610	0.360687	0.0601	-0.9410
SIRE	28	-295.103546	-10.539412	0.360687	0.0	-0.8800
DAM	58	-1050.602452	-18.113835	-2.056335	-0.9885	-0.9758
ERROR	522	-1905.033786	-3.649488	-3.649488	-0.9373	-0.9373

COVARIANCE OF VARIABLE OPROTEIN WITH OFAT

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	608	-12337.615505	-20.292131	1.102277	0.0496	-0.9621
SIRE	28	-1329.010057	-47.464645	1.102277	0.0	-0.9646
DAM	58	-4035.525262	-70.612470	-8.195574	-0.9847	-0.9784
ERROR	522	-6913.082186	-13.243452	-13.243452	-0.9578	-0.9578

Appendix B. Continued.

COVARIANCE OF VARIABLE DPROTEIN WITH LENGTH

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	608	4453.624039	7.325940	11.251240	0.1192	0.0799
SIRE	28	3828.942135	136.747933	4.407353	0.0	0.3673
DAM	56	2563.224762	44.193530	6.843868	0.2926	0.1960
ERROR	522	-1936.542857	-3.713684	-3.713684	-0.0644	-0.0644

COVARIANCE OF VARIABLE DPROTEIN WITH WTGMS

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	608	11754.795995	19.349993	25.540761	0.1298	0.1012
SIRE	28	10296.313043	367.725466	13.897062	0.0	0.4713
DAM	58	4401.456095	75.887174	11.643700	0.2519	0.1666
ERROR	522	-2932.973143	-5.618722	-5.618722	-0.0464	-0.0464

COVARIANCE OF VARIABLE DPROTEIN WITH K

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	608	18.005681	0.029615	0.071943	0.0676	0.0370
SIRE	28	29.059419	1.037836	0.062530	0.0	0.4290
DAM	58	-15.967367	-0.275299	-0.040673	-0.2515	-0.1504
ERROR	522	4.913529	0.009413	0.009413	0.0164	0.0164

Appendix B. Continued.

COVARIANCE OF VARIABLE DPROTEIN WITH KLOG

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	608	4.852074	0.007980	0.018168	0.0950	0.0429
SIRE	28	7.621678	0.272203	0.016116	0.0	0.4439
DAM	58	-3.841144	-0.066227	-0.009754	-0.2412	-0.1522
ERROR	522	1.071541	0.002053	0.002053	0.0158	0.0158

COVARIANCE OF VARIABLE DPROTEIN WITH ASHLOG

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	608	-12.132676	-0.019955	0.003091	0.0156	-0.1041
SIRE	28	-0.668701	-0.023882	0.003091	0.0	-0.0541
DAM	58	-5.150404	-0.088800	-0.010958	-0.1825	-0.1590
ERROR	522	-6.313574	-0.012095	-0.012095	-0.0893	-0.0893

COVARIANCE OF VARIABLE ASH WITH WFAT

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	608	-5.222948	-0.008590	0.008393	0.0258	-0.0274
SIRE	28	-2.186043	-0.078073	-0.005986	0.0	-0.1313
DAM	58	2.763038	0.047639	0.008393	0.1019	0.0578
ERROR	522	-5.799943	-0.011111	-0.011111	-0.0462	-0.0462

Appendix B. Continued.

COVARIANCE OF VARIABLE ASH WITH DFAT

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	608	-75.906642	-0.124846	0.603672	0.0030	-0.1071
SIRE	28	-10.342933	-0.369390	-0.013309	0.0	-0.1512
DAM	58	-5.214538	-0.089906	0.003672	0.0112	-0.0280
ERROR	522	-60.349171	-0.115611	-0.115611	-0.1346	-0.1346

COVARIANCE OF VARIABLE ASH WITH LENGTH

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	608	305.703136	0.502801	0.529285	0.1033	0.0993
SIRE	28	23.112184	0.825435	-0.025954	0.0	0.0447
DAM	58	79.486667	1.370460	0.140196	0.1521	0.1368
ERROR	522	203.104286	0.389089	0.389089	0.1092	0.1092

COVARIANCE OF VARIABLE ASH WITH WTGMS

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	608	730.158358	1.200918	1.204353	0.1127	0.1137
SIRE	28	92.186358	3.292370	0.028046	0.0	0.0850
DAM	58	156.797429	2.703404	0.254516	0.1397	0.1336
ERROR	522	481.174571	0.921790	0.921790	0.1231	0.1231

Appendix B. Continued.

COVARIANCE OF VARIABLE ASH WITH K

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	608	0.900494	0.001481	0.002370	0.0532	0.0335
SIRE	28	0.548246	0.019580	0.001161	0.0	0.1630
DAM	58	-0.278552	-0.004803	-0.000859	-0.1346	-0.0590
ERROR	522	0.630800	0.001208	0.001208	0.0341	0.0341

COVARIANCE OF VARIABLE ASH WITH KLOG

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	608	0.268105	0.000441	0.000651	0.0627	0.0429
SIRE	28	0.134717	0.004811	0.000279	0.0	0.1581
DAM	58	-0.060761	-0.001048	-0.000203	-0.1273	-0.0542
ERROR	522	0.194149	0.000372	0.000372	0.0463	0.0463

COVARIANCE OF VARIABLE ASH WITH ASHLOG

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	608	6.372652	0.010481	0.010644	0.9900	0.9899
SIRE	28	0.609272	0.021760	-0.000145	0.0	0.9927
DAM	58	1.438165	0.024796	0.002359	0.9967	0.9930
ERROR	522	4.325195	0.008286	0.008286	0.9892	0.9892

Appendix B. Continued.

COVARIANCE OF VARIABLE WEAT WITH DEAT

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	608	3365.743121	5.535762	5.914199	0.9620	0.9541
SIRE	28	296.170678	10.577524	-0.370159	0.0	0.9162
DAM	58	1064.349636	18.350857	2.072776	0.9961	0.9843
ERROR	522	2005.222757	3.841423	3.841423	0.9466	0.9466

COVARIANCE OF VARIABLE WEAT WITH LENGTH

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	608	232.553432	0.382489	2.547397	0.0976	0.0152
SIRE	28	-543.575616	-19.413415	-0.469923	0.0	-0.2223
DAM	58	-553.612391	-9.545041	-1.727491	-0.2954	-0.1639
ERROR	522	1329.741429	2.547397	2.547397	0.1513	0.1513

COVARIANCE OF VARIABLE WEAT WITH WIGHS

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	608	489.540821	0.805166	5.182905	0.0952	0.0153
SIRE	28	-1487.980227	-53.142151	-1.932914	0.0	-0.2903
DAM	58	-727.955238	-12.550952	-2.535408	-0.2192	-0.1066
ERROR	522	2705.476286	5.182905	5.182905	0.1466	0.1466

Appendix B. Continued.

COVARIANCE OF VARIABLE WFAT WITH K

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	608	3.781353	0.006219	0.017826	0.0785	0.0283
SIRE	28	-4.164823	-0.148744	-0.011861	0.0	-0.2621
DAM	58	5.819876	0.100343	0.013753	0.3398	0.2122
ERROR	522	2.126300	0.004073	0.004073	0.0243	0.0243

COVARIANCE OF VARIABLE WFAT WITH KLOG

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	608	0.859004	0.001413	0.004303	0.0614	0.0276
SIRE	28	-1.059764	-0.037849	-0.002954	0.0	-0.2631
DAM	58	1.403342	0.024196	0.003315	0.3279	0.2153
ERROR	522	0.515426	0.000987	0.000987	0.0260	0.0260

COVARIANCE OF VARIABLE WFAT WITH ASHLOG

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	608	0.019730	0.000032	0.001716	0.0413	0.0006
SIRE	28	-0.225299	-0.008046	-0.000913	0.0	-0.0777
DAM	58	0.651632	0.011235	0.001716	0.1143	0.0774
ERROR	522	-0.406603	-0.000779	-0.000779	-0.0197	-0.0197

Appendix B. Continued.

COVARIANCE OF VARIABLE DFAT WITH LENGTH

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	608	-4096.905404	-6.738331	3.676653	0.0380	-0.0720
SIRE	28	-3486.694532	-124.524805	-3.853050	0.0	-0.3470
DAM	58	-2529.423810	-43.610755	-6.755344	-0.2901	-0.1926
ERROR	522	1919.212857	3.676653	3.676653	0.0612	0.0612

COVARIANCE OF VARIABLE DFAT WITH WTGMS

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	608	-10521.884814	-17.305732	5.373822	0.0266	-0.0087
SIRE	28	-9233.311957	-329.761141	-12.341904	0.0	-0.4345
DAM	58	-4093.707714	-70.581167	-10.850713	-0.2358	-0.1542
EPROR	522	2805.134857	5.373822	5.373822	0.0426	0.0426

COVARIANCE OF VARIABLE DFAT WITH K

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	608	-10.891062	-0.017564	0.947109	0.0560	-0.0215
SIRE	28	-25.271747	-0.902562	-0.058309	0.0	-0.3870
DAM	58	18.671543	0.321923	0.047109	0.2924	0.1751
ERROR	522	-4.090857	-0.007837	-0.007837	-0.0131	-0.0131

COVARIANCE OF VARIABLE DFAT WITH KLOG

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	608	-3.139996	-0.005164	0.011282	0.0576	-0.0272
SIRE	28	-6.595183	-0.235542	-0.014885	0.0	-0.3985
DAM	58	4.466106	0.077036	0.011282	0.2803	0.1767
ERROR	522	-1.012919	-0.001940	-0.001940	-0.0143	-0.0143

COVARIANCE OF VARIABLE DFAT WITH ASHLOG

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	608	-9.849185	-0.016199	0.001375	0.0068	-0.0328
SIRE	28	-1.142609	-0.040807	-0.001641	0.0	-0.0955
DAM	56	-0.368353	-0.006351	0.001375	0.0230	-0.0113
ERROR	522	-0.338424	-0.015974	-0.015974	-0.1131	-0.1131

COVARIANCE OF VARIABLE LENGTH WITH WTGMS

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	608	0.48314250D 06	0.79466229D 03	0.80232970D 03	0.9379	0.9370
SIRE	28	0.15333720D 06	0.54765390D 04	0.19695270D 03	0.9711	0.9625
DAM	58	77738.723810	1340.322824	122.490973	0.9473	0.9377
ERROR	522	0.25206650D 06	0.48290600D 03	0.48288600D 03	0.9221	0.9221

COVARIANCE OF VARIABLE LENGTH WITH K

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	608	-261.159507	-0.429539	0.180147	0.0504	-0.1211
SIRE	28	56.613826	2.021922	0.180147	0.3237	0.1146
DAM	58	-102.147619	-1.761166	-0.192584	-0.4253	-0.3066
ERROR	522	-215.625714	-0.413076	-0.413076	-0.1664	-0.1664

COVARIANCE OF VARIABLE LENGTH WITH KLOG

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	608	-57.922450	-0.095267	0.049441	0.0594	-0.1154
SIRE	28	16.842635	0.601523	0.049441	0.3368	0.1345
DAM	58	-25.331362	-0.436748	-0.048864	-0.4320	-0.3200
ERROR	522	-49.433723	-0.094701	-0.094701	-0.1686	-0.1686

COVARIANCE OF VARIABLE LENGTH WITH ASHLOG

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	608	50.226502	0.082609	0.089991	0.1045	0.0972
SIRE	28	1.768747	0.063170	-0.007414	0.0	0.0196
DAM	58	12.694091	0.218864	0.021479	0.1279	0.1241
ERROR	522	35.763664	0.068513	0.068513	0.1169	0.1169

COVARIANCE OF VARIABLE WTGMS WITH K

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	608	849.905438	1.397871	1.532146	0.2057	0.1889
SIRE	28	375.301010	13.403607	0.633669	0.5368	0.3625
DAM	58	5.599857	0.096549	-0.114561	-0.1280	0.0083
ERROR	522	469.004571	0.898476	0.898476	0.1724	0.1724

COVARIANCE OF VARIABLE WTGMS WITH KLOG

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	608	207.603619	0.341453	0.375579	0.2165	0.1983
SIRE	28	100.181921	3.577926	0.176201	0.5466	0.3818
DAM	58	0.214392	0.003696	-0.026812	-0.1289	0.0013
ERROR	522	107.207305	0.205378	0.205370	0.1741	0.1741

COVARIANCE OF VARIABLE WTGMS WITH ASHLOG

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	608	122.355308	0.201242	0.203227	0.1131	0.1135
SIRE	28	11.631961	0.415427	-0.001633	0.0	0.0616
DAM	58	26.083703	0.449719	0.041082	0.1237	0.1262
ERROR	522	84.639645	0.162145	0.162145	0.1318	0.1318

COVARIANCE OF VARIABLE K WITH KLOG

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	608	4.340195	0.007138	0.007174	0.9912	0.9912
SIRE	28	0.311606	0.028986	0.000856	1.0018	0.9974
DAM	58	0.636761	0.011013	0.000782	0.9995	0.9937
ERROR	522	2.889828	0.005536	0.005536	0.9903	0.9903

COVARIANCE OF VARIABLE K WITH ASHLOG

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	608	0.174849	0.000288	0.000403	0.0537	0.0388
SIRE	28	0.087568	0.003127	0.000175	0.0	0.1494
DAM	58	-0.031573	-0.000544	-0.000110	-0.0949	-0.0380
ERROR	522	0.118855	0.000228	0.000228	0.0390	0.0390

COVARIANCE OF VARIABLE KLOG WITH ASHLOG

COVARIANCE SOURCE	D.F.	SUM OF PRODUCTS	MEAN PRODUCTS	COVARIANCE COMPONENT	VARIANCE COMPONENT CORRELATION	MEAN SQUARE CORRELATION
TOTAL	609	0.050637	0.000083	0.000110	0.0631	0.0483
SIRE	28	0.021313	0.000761	0.000042	0.0	0.1435
DAM	58	-0.650706&D-02	-0.11219080-03	-0.25833230-04	-0.0089	-0.0330
ERROR	522	0.035831	0.000069	0.000069	0.0520	0.0520